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Overview of the North American terrestrial gastropod fauna*

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Abstract: A revised database of terrestrial gastropods from North America north of Mexico was assembled in the spring of 2012, which included not only all likely species-level entities, updated family and naturalized exotic assignments, but also shell and body size data. Analyses of these reveal that: (1) the fauna represents approximately 1,200 species, and is dominated by the Polygyridae, Helminthoglyptidae, and Vertiginidae. This number is surprisingly small, with other land masses of ½ to 1/100th the size possessing a larger fauna; (2) naturalized species make up 6% of the total fauna; (3) while slugs represent only 7% of the native fauna, they constitute over 1/3 of the naturalized fauna; (4) the accumulation curve for recognized species is sigmoidal, with current rates being the lowest experienced in 200 years. As a result, it appears that only 150–300 net additional taxa may await description, with the principle future taxonomic activity being revisionary work; (5) like other faunas, both native and naturalized land snails in North America possess bimodal height/width ratios; (6) native land snails possess a bimodal, right-skewed biovolume distribution along a log axis, which differs greatly from the unimodal left-skewed distribution typical of many other taxa groups; and, (7) the distribution of species within families and genera, and of the number of species described by a given researcher all possess Power Law/Log Normal distributions characteristic of complex adaptive systems.

Key words: Body size patterns, complex systems, diversity, land snail, macroecology

With the publication of the last volume of the "Land Mollusca of North America (North of Mexico)" by Henry Pilsbry in 1948, this fauna became the first to be taxonomically well-described at the continental level. However, since this time efforts to maintain and update his work have been principally limited to Leslie Hubricht's county-scale range maps for eastern U.S.A. species (Hubricht 1985) and two checklists of common and scientific names for the Mollusca of the United States and Canada published by the American Fisheries Society (Turgeon *et al.* 1988, 1998). While representing a massive undertaking, the latter include only very transcribed ecological information (limited to native or alien status), use a now outdated family-level taxonomy, and do not consider any taxa listed by Pilsbry (1948) or subsequent workers as subspecies. Because Hubricht (1985) tended to split these entities into separate species, this is less of an issue for the eastern U.S.A. fauna. However, since little revisionary work has been conducted on the western U.S.A. fauna, a strong potential exists for this policy to lead to underreporting of valid species in this region. And, obviously, no species described in the almost 15 years since publication of the second edition of Turgeon *et al.* were included.

To address these concerns, an updated list of the North American terrestrial gastropod fauna north of Mexico was assembled during the spring of 2012. It not only updates family level taxonomy to current concepts, but also includes all likely species that Pilsbry (1948) lists as subspecies, and includes all species described through May 2012. This dataset also records median shell/body size dimensions from the published literature and from this calculates shell biovolume for each entry. As a result, a current and modern overview of this terrestrial gastropod fauna can be constructed.

MATERIALS AND METHODS

Faunistic enumeration

Only species having native or naturalized populations in North America north of Mexico were considered; species occurring south of the U.S.A. boundary are considered part of the Central American fauna for purposes of this work. While an initial listing of the Central American fauna is now available (Thompson 2011), these taxa have not been included because of: (1) the historical limitation of previous works (*e.g.*, Pilsbry 1948, Turgeon *et al.* 1998) to North America north of Mexico; (2) the much poorer understanding of alpha-level taxonomy in the Central American fauna; and (3) their often distinct evolutionary affinities. Although a number of North American

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elements extend south into at least northern Mexico (*e.g.*, the genus *Ashmunella* Pilsbry and Cockerell, 1899 and the subgenus *Immersidens* Pilsbry and Vanatta, 1900 within the genus *Gastrocopta* Wollaston, 1878), and some Caribbean and Central American elements extend north into the southern U.S.A. (*e.g.*, the Urocoptidae and Orthalicidae), the artificial demarcation used here is similar to those erected by molluscan biogeographers elsewhere, such as in Eurasia where European, Asian, east Asian, and south Asian faunas are usually considered as largely separate entities (Naggs and Raheem 2005, Pokryszko and Cameron 2005).

The initial point of departure was all terrestrial gastropod entries from Turgeon *et al.* (1998). To this were added all subsequently described species as determined via the *Zoological Record* database. Additionally, all species listed by Hubricht (1985) – but not by Turgeon *et al.* (1998) – were included. Most of these represent dead shells limited to drift along the south Texas Gulf Coast. While their presence in North America may be due to long-distance rafting from extralimital colonies (the apparent rationale used to justify exclusion), it seems equally likely that they were sourced from nearby, localized extant colonies. Inclusion of these taxa, thus, seems prudent to ensure that no extant species were ignored. The list was also expanded to include all subspecies-level entities from Pilsbry (1948) that appear, based on their unique shell features, ranges, and/or ecological preferences, to represent valid species-level entities. Pilsbry (1948) took a conservative approach to species designations, and chose to lump numerous forms as subspecies until appropriate data existed to falsify these hypotheses. As a result, many species-level entities were listed by Pilsbry (1948) as subspecies, as has been recently shown within the Polygyridae (Emberton 1988), Helminthoglyptidae (Lang and Gilbertson 2010), and Vertiginidae (Nekola *et al.* 2009). However, not all of Pilsbry's subspecies concepts appear to warrant species-level listing: examples are the minor shell variants limited to specific canyons within a given species range, as demonstrated not only by subspecies described within *Ashmunella proxima* Pilsbry, 1905 and *A. levettei* (Bland, 1881) of the Chiricahua and Huachuca ranges of southeastern Arizona, respectively, but also in various species within the genus *Oreohelix* Pilsbry, 1904.

Finally, fourteen undescribed new species encountered by the author during field sampling across North America have also been included. These represent six *Vertigo* Müller, 1774, plus single representatives of *Columella* Westerlund, 1878, *Daedalochila* Beck, 1837, *Glyphyalinia* von Martens, 1892, *Hawaiia* Gude, 1911, *Helicodiscus* Morse, 1864, *Paravitrea* Pilsbry, 1898, *Punctum* Morse, 1864, and *Succinea* Draparnaud, 1801.

Taxonomic information

The authorship of each entry was recorded, as was the year of description. Family assignments were updated to Bouchet and Rocroi (2005), with the placement of genera into these families basically following Schileyko's 1998–2006 "*Treatise on Recent Terrestrial Pulmonate Molluscs*" as used in the Academy of Natural Sciences of Drexel University (ANSP) collection.

Ecological information

Species native or naturalized status was based largely on Turgeon *et al.* (1998) with subsequent additions and changes based on Nekola and Coles (2010). Species with documented pre-Columbian occurrences in North America are treated as native even though some (*e.g.*, *Cepaea hortensis* Müller, 1774) may represent earlier European colonizations via the Norse or Basque. Each entry was assigned either as a slug or snail, with semislugs being classed as snails due their presence of a relatively large external shell. Body dimensions for each entry was determined from either the published literature, or in the case of undescribed taxa from lots held in the Nekola collection. For snails, median reported shell height (mm), width (mm) and proportion of shell height which is columnar were recorded. Shell biovolume in mm^3 was then estimated as a conic-section placed on top of a column (McClain and Nekola 2008) using the formula:

$$V = \pi r^2 ht + \left[\frac{\pi r^2 h(1-t)}{3}\right]$$

where: V = biovolume in cubic mm; h = height; r = width/2; t = taper proportion varying from 1 = completely columnar shell height to 0 = completely tapered shell height.

For slugs, the median width and diameter in mm was recorded for relaxed individuals. Slug biovolume in cubic mm was simply estimated as a cylindrical column:

$$V = \pi r^2 h$$

Analyses

Richness at the species, genus, and family level were calculated for the native and naturalized fauna. The largest families and genera in terms of species richness were also determined. The accumulation of currently accepted names over time was plotted for the native fauna, with the mean number of described entities calculated for five different chronological eras (1774–1815, 1816–1889, 1890–1942, 1943–1990, and 1991–present) whose boundaries were based upon rate discontinuities in the accumulation graph. The number of species described per author was also determined within the native fauna. Two general analyses were conducted on the biovolume data: First, the body-size spectrum of the native and naturalized faunas were displayed for snails and slugs via histograms based on 41 $\log_2$ volume classes with bins starting at -2.5 and increasing by 0.5 $\log_2$ units to 18.0. The first bin value ranged from -2.5 to -2.0 (~0.18–0.25 mm^3) and

the last bin from 17.5–18.0 (185,363.8–262,144 mm^3). The number of species were tabulated within each log_2 volume bin and plotted. Second, a histogram of natural log-transformed height-width ratios was generated for both the native and naturalized land snail faunas. Log transformation was used along the height-width axis as it allowed for a similar spread in values for shells less than or greater than 1.0. Without this transform, the range of variation for shells wider than tall would be compressed into ¼ of the range covered by shells that were taller than wide, complicating analysis.

RESULTS

Fauna size and composition

A total of 1,204 terrestrial gastropod species level entities were recorded (Table 1; Appendix 1), representing 170 genera and 51 families; 1,128 species, 136 genera, and 41 families are native to the continent, or at least of pre-Columbian occurrence. Seventy six of these had been previously recorded as subspecies by Pilsbry (1948). Across the native fauna, 84 species, 28 genera, and eight families represent slugs. The naturalized fauna represents 76 species, 46 genera, and 26 families, of which 26 species, 12 genera, and six families are slugs.

By far the most diverse family represented in the native fauna (Table 2) is the Polygyridae with 271 species (24.0% of native fauna), followed by the Helminthoglyptidae (178; 15.8%), Vertiginidae (102; 9.0%), Oreohelicidae (84; 7.4%), and Pristilomatidae (65; 5.8%). The ten richest families contain a total of 884 likely species-level entities, or 78.4% of the total fauna. On the other side of the distribution, one family (Cochlicopidae) is represented by only three species, four families (Charopidae, Pomatiidae, Pomatiopsidae, and Vitrinidae) by only two species, and six families (Cepolidae, Ferrussaciidae, Helicidae, Oleacinidae, Sagdidae, and Veronicellidae) by only a single native species. The most diverse genus in the fauna is *Oreohelix* (79 species, or 7.0% of the native fauna) followed by *Sonorella* Pilsbry, 1900 (71; 6.3%), *Helminthoglypta* Ancey, 1887 (70; 6.2%), *Vertigo* (65; 5.8%), and *Ashmunella* (53; 4.7%). The ten most diverse genera contain 498 species, or 44.1% of the total fauna. On the other side of the distribution, eleven genera are represented by only three species, 17 genera by only two species, and 45 genera by on a single one native species.

Eight families (Arionidae, Helicidae, Hygromiidae, Limacidae, Oxychilidae, Pleurodontidae, Subulinidae, and Veronicellidae) constitute almost three-quarters of the post-Columbian naturalized fauna (Table 2B). On the other end of the distribution, one family is represented by only three species, three families by only two species, and fourteen families by only a single naturalized species. By far and away *Arion* Férussac, 1819 represents the most diverse genus of naturalized species (10 species, or 14.1% of the naturalized fauna), followed equally by *Lamellaxis* Strebel and Pfeffer, 1882, *Limax* Linné, 1758, and *Oxychilus* Fitzinger, 1833 (4; or 5.6% each). Two genera are represented by only three species, eight genera by only two species, and 32 genera by only a single naturalized species.

Alpha-level taxonomy history

Since the first description of a native North American terrestrial gastropod species by Danish naturalist Otto Friedrich Müller in 1774, a total of 149 investigators have

Table 1. Overview of North American terrestrial gastropod fauna.

	Species	Genera	Families
Total	1204	170	51
(slugs)	84	28	8
Native	1128	136	41
(slugs)	58	18	6
Introduced	76	46	26
(slugs)	26	12	6

Table 2. Most diverse families and genera at the species level.

A. Native fauna

Family	Species	Genera	Species
Polygyridae	271	*Oreohelix*	79
Helminthoglyptidae	178	*Sonorella*	71
Vertiginidae	102	*Helminthoglypta*	70
Oreohelicidae	84	*Vertigo*	65
Pristilomatidae	64	*Ashmunella*	53
Succineidae	48	*Paravitrea*	42
Oxychilidae	45	*Daedalochila*	34
Gastrodontidae	35	*Stenotrema* Rafinesque, 1819	29
Urocoptidae	31	*Triodopsis* Rafinesque, 1819	28
Discidae	26	*Gastrocopta*	27

B. Naturalized Introduced fauna:

Family	Species	Genera	Species
Arionidae	10	*Arion*	10
Subulinidae	8	*Lamellaxis*	4
Hygromiidae	8	*Limax*	4
Helicidae	7	*Oxychilus*	4
Veronicellidae	7		
Limacidae	5		
Oxychilidae	4		
Pleurodontidae	4		
Subulinidae	4		

contributed to the naming of the native fauna. The top ten contributors include (Table 3): Henry A. Pilsbry, James H. Ferriss, Leslie Hubricht, Thomas Say, S. Stillman Berry, Victor Sterki, Walter B. Miller, Thomas B. Bland, Augustus A. Gould, and William G. Binney. On the other side of this distribution fourteen individuals have contributed to the description of only three species, twenty to only two species , and 61 to only a single native species.

The accumulation of recognized native North American taxonomic descriptions over time exhibits a sigmoidal pattern (Fig. 1). Initial description rates were low (0.2 species / year), and restricted to charismatic or Holarctic species described by European researchers. Beginning with Thomas Say in 1816, North American malacologists began in earnest the naming of their fauna, describing through the 1880s and average of 4.4 species a year. The most productive era began in 1890 with the start of Pilsbry's career at ANSP: through 1942 an average of 10.3 new North American terrestrial gastropod species would be described per year. These rates decreased to an average of 4.6 per year from 1943–1990, and have decreased further to an average of 1.8 per year for the last decade of the 20th Century through the first dozen years of the new millennium.

Body Size and Shell Shape Patterns

Native North American land snails (Table 4a) range in size from the 1.1 mm x 0.6 mm *Punctum minutissimum* (I. Lea, 1841) to the 34 mm x 61 mm *Orthalicus floridensis* Pilsbry, 1889. Native slugs range in size from the 4.0 mm x 2.0 mm *Deroceras leave* (Müller, 1774) to the 222 mm x 37 mm *Ariolimax columbianus* (Gould, 1851). While 264 native species (24.7% of total) have a maximum dimension < 5 mm, 201 (18.8%) range from 5 ≤ 10 mm, 403 (37.7%) from 10 ≤ 20 mm, 197 (18.4%) from 20 ≤ 40 mm, and 5 (0.5%) are ≥ 40 mm. One native slug (1.7% of all native slugs) has a maximum dimension < 5 mm, while five (8.6%) range from 5 ≤ 10 mm, 15 (25.9%) from 10 ≤ 20 mm, 18 (31.0%) from 20 ≤ 40 mm, and 19 (32.8%) are ≥ 40 mm.

Naturalized land snails (Table 4b) range in size from the 0.9 mm x 1.8 mm *Carychium minimum* Müller, 1774 to the 36 mm x 35 mm *Helix pomatia* Linnaeus, 1758. Naturalized exotic slugs range in size from the 20.0 mm x 3.3 mm *Arion intermedius* Normand, 1852 to the 150 mm x 25 mm *Limax maximus* Linnaeus, 1758. While eleven naturalized land snails (22.07% of total) have a maximum dimension < 5 mm, thirteen (26.0%) range from 5 ≤ 10 mm, fourteen (28.0%) from 10 ≤ 20 mm, and twelve (24.0%) from 20 ≤ 40 mm. No naturalized North American snail equals or exceeds 40 mm in maximum dimension. No naturalized exotic slug has maximum dimensions < 20mm. Eight naturalized slugs (30.8% of all naturalized slugs) have a maximum dimension from 20 ≤ 40 mm while eighteen (69.2%) are ≥ 40 mm.

Biovolume represents a more accurate expression of body size because it considers both height and width. Native North American land snails range from the 0.18 mm^3 *Carychium nannodes* G. H. Clapp, 1905 to the 33,230 mm^3 *Orthalicus floridensis*. The body size spectrum (Fig. 2a) exhibits a bimodal distribution with one mode ranging from 1.4–2.0 mm^3, and the other from 512–724 mm^3. The minimum between these two modes occurs from 16–22.6 mm^3. The right mode exhibits a clear left-skew, although the left mode appears approximately log-normal. Native slugs range from the 7.9 mm^3 *Udosarx lyrata* Webb, 1959 to the ~240,000 mm^3 *Ariolimax columbianus*, with the mode occurring at 362–512 mm^3. The biovolume distribution of these species was approximately log-normal, but shifted slightly to the right of land snails.

Naturalized land snails range from the 0.51 mm^3 *Carychium tridentatum* (Risso, 1826) to the 23,091 mm^3 *Helix pomatia*. The body size spectrum (Fig. 2b) exhibits essentially a uniform distribution across this range. Naturalized exotic slugs range from the 171 mm^3 *Arion intermedius* to the ~74,000 mm^3 *Limax maximus*, with the mode occurring at 362–512 mm^3. The biovolume distribution of these species was approximately log-normal, but shifted to the right of land snails.

Lastly, the height vs. width ratio for both native and naturalized North American land snails is also strongly bimodal (Fig. 3) with the left mode ranging from 0.50–0.67 (1:2–2:3) in both and from 1.8–2.2 (9:5–11:5) in the native and from 3.3–4.1 (10:3–4:1) in the naturalized faunas. Almost no native or naturalized species possess shell height vs. width ratios ranging from 1.0–1.5 (1:1–3:2).

Table 3. Most prolific describers of the North American terrestrial gastropod fauna.

Individual	Species Described	Inclusive Years	Emphasis
Henry A. Pilsbry	305	1889–1953	Whole continent
James H. Ferriss	82	1900–1925	SW U.S.A.
Leslie Hubricht	79	1938–1983	E U.S.A.
Thomas Say	51	1816–1831	E. North America
S. Stillman Berry	46	1916–1955	California
Victor Sterki	35	1889–1919	Whole continent (pupillids)
Walter B. Miller	31	1966–2000	W U.S.A. (polygyrids and helminthoglyptids)
Thomas B. Bland	28	1856–1883	S and W U.S.A.
Augustus A. Gould	26	1840–1855	Whole continent
William G. Binney	26	1857–1892	Whole continent

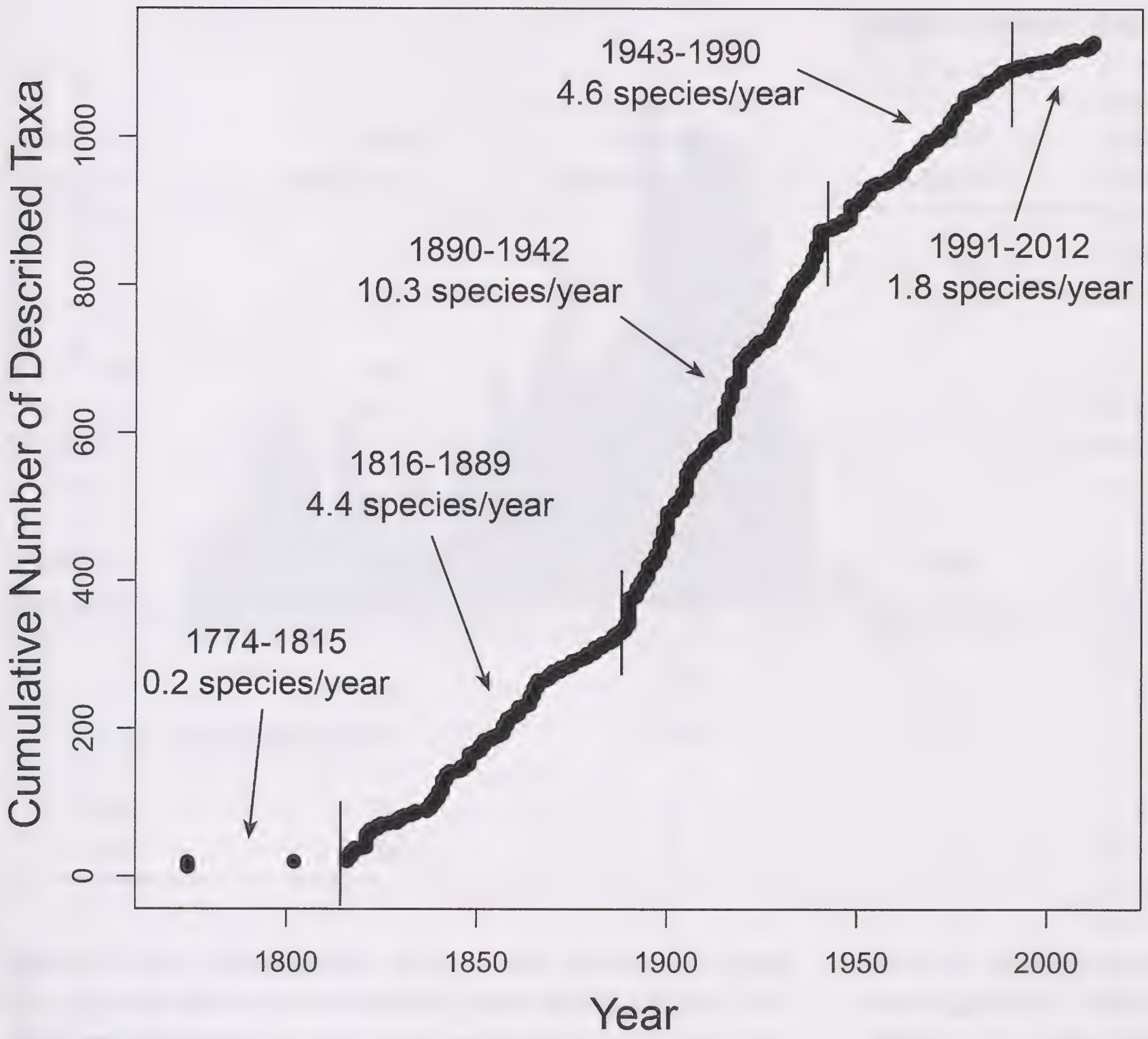

Figure 1: Accumulation curve for recognized native North American terrestrial gastropod species over time.

DISCUSSION

It is a testament to Pilsbry that over 60 years after publication of his North American monograph, in broad brushstrokes his summary of the terrestrial gastropod fauna remains largely unchanged: the fauna includes approximately 1,200 species, with the Polygyridae and Helminthoglyptidae dominating. Yet, there are a number of important additional insights which can be drawn:

Faunistic summary

First, an often overlooked but crucial component of the fauna are the vertiginids, which constitute the third most diverse family, with the genera *Vertigo* and *Gastrocopta* being the fourth and tenth most-speciose genera, respectively. Native vertiginids encompass approximately 1/3 of the total global richness for the entire family (Liggia 2012) and at least 2/3 of global richness for the genus *Vertigo* (Nekola *et al.* 2009), making North America a globally important biodiversity center for the group. At the site scale, the importance of this family is even greater: vertiginids represent roughly 1/3 of the species and individuals found on an average site across the continent, with regional values ranging from 56% of species and 60% of individuals on an average Alaskan site to 17% of species and 21% of individuals on an average Florida site (Nekola, *unpub. data*). The next most important family at the site scale (the Gastrodontidae) possesses values approximately three times smaller. Thus, whether the North American terrestrial gastropod fauna should be characterized as being dominated by polygyrids, helminthoglyptids or vertiginids is squarely dependent upon the observational scale: while the former two are most important at the regional to continental scale, on individual sites the vertiginids dominate.

Second, the overall proportion of exotic species is relatively low, representing only approximately 6% of the total fauna. However, this level can locally range much higher, especially at low latitudes. Many disturbed sites in south Florida, for instance, are dominated by a host of naturalized exotics in the Bradybaenidae, Helicarionidae, Orthalicidae, Pleurodontidae, Streptaxidae, and Subulinidae. Helicids and hygromiids may also be locally important components of disturbed faunas in both the northeast and southwest. The importance of naturalized exotics is especially notable in the slug fauna: while slugs represent only 7% of the entire native fauna, they represent 1/3 of the introduced fauna, with fully ten species within the genus *Arion* having become established on the continent. It also seems likely that additional naturalized species may exist within the fauna, even though historically having been considered native. For instance, *Pupilla muscorum* Linnaeus, 1758, is represented in North America by naturalized European populations which are restricted to the urban corridor of the Northeast west through the Great Lakes. Individuals occurring along roadside verges in Cedar Rapids, Iowa have identical mitochondrial and nuclear haplotypes to material originating from Brno in the Czech Republic (Nekola, *unpub. data*). Northern and western populations of *Pupilla 'muscorum'*, however, represent native taxa that are not closely related to this species (Nekola *et al.* in review). It seems likely that similar mixes of native and introduced populations will be uncovered in other anthropophilic Holarctic 'species', such

Table 4. Body size distribution across the North American fauna.

A. Native Species

Maximum Dimension	Minute (< 5 mm)	Small (5–10 mm)	Medium (10–20 mm)	Large (20–40 mm)	Very Large (40+ mm)
Land Snails					
Number of taxa	264	201	403	197	5
Percent	24.7	18.8	37.7	18.4	0.5
Slugs					
Number of taxa	1	5	15	18	19
Percent	1.7	8.6	25.9	31.0	32.8

B. Naturalized Species

Maximum Dimension	Minute (< 5 mm)	Small (5–10 mm)	Medium (10–20 mm)	Large (20–40 mm)	Very Large (40+ mm)
Land Snails					
Number of taxa	11	13	14	12	0
Percent	22.0	26.0	28.0	24.0	0
Slugs					
Number of taxa	0	0	0	8	18
Percent	0	0	0	30.8	69.2

as *Cochlicopa lubrica* (Müller, 1774), *Cochlicopa lubricella* (Porro, 1838), *Deroceras laeve* (Müller, 1774), *Vallonia costata* (Müller, 1774), *Vallonia excentrica* Sterki, 1893, and *Vallonia pulchella* (Müller, 1774).

Third, even though the North America terrestrial gastropod fauna supports roughly twice the number of species as better known invertebrate groups such as butterflies and skippers (Scott 1986), it is surprisingly depauperate as compared to other terrestrial gastropod faunas. Of the estimated 35,000 total global terrestrial gastropod species (Barker 2001), approximately 3,600 occur in Europe (Bank *et al.* 1998), more than 2,500 in Australia (John Stanisic, *pers. comm.*), and 1,400 in New Zealand (Barker and Mayhill 1999). Thus, North America supports fewer species than land masses ranging from one-half to 1/100th of its size.

Last, it is important to emphasize that these patterns are subject to change as additional data becomes available. For instance, in the time between initial drafting and editorial acceptance of this manuscript, preliminary results (Nekola, *unpub. data*) revealed that considerable revision of higher taxonomic concepts will likely be necessary within the Pupillidae and Vertiginidae. In particular, the Vertiginidae do not appear to be a distinct family, with most members being distributed throughout the Pupillidae. And, other families, such as the Valloniidae, also appear to represent pupillids. As a result, the importance of the Pupillidae within the North American fauna is likely even greater than indicated above. Additionally, some putative vertiginids—such as the genus *Columella*—are actually chondrinids. And, it is also clear that the genus *Vertigo* itself has been badly oversplit and actually includes other genera such as *Sterkia* Pilsbry, 1898. These data also strongly suggest that *Vertigo* AK2 and *Vertigo* AK4 represent populations of the Eurasian *V. ronnebyensis* Westerlund, 1871 and *V. microspharea* Schileyko, 1984, respectively. However, until such preliminary findings have been vetted through the review process, they must be ignored within the context of this work.

Taxonomic activities

These analyses document that the shape of the recognized species vs. description year curve is sigmoidal, with current rates for new species descriptions being the lowest seen in almost 200 years. It is important to note, however, that the asymptotic number of recognized species is only being approached but has not yet been met. As a result it seems likely that there are another 150-300 additional net species in the fauna awaiting description. These taxa, however, will likely be named at ever decreasing rates.

The taxonomic activity that will take on increasing precedence is, thus, revisionary work, in which the true status of the various named entities are subjected to empirical validation. Because of their relatively easy mutability, conchological features alone may not be adequate to demarcate species-level groups. For instance, the variable presence of an angular and basal lamella, of the length and degree of inset of the upper palatal lamella, depth of depression over the palatal lamellae,

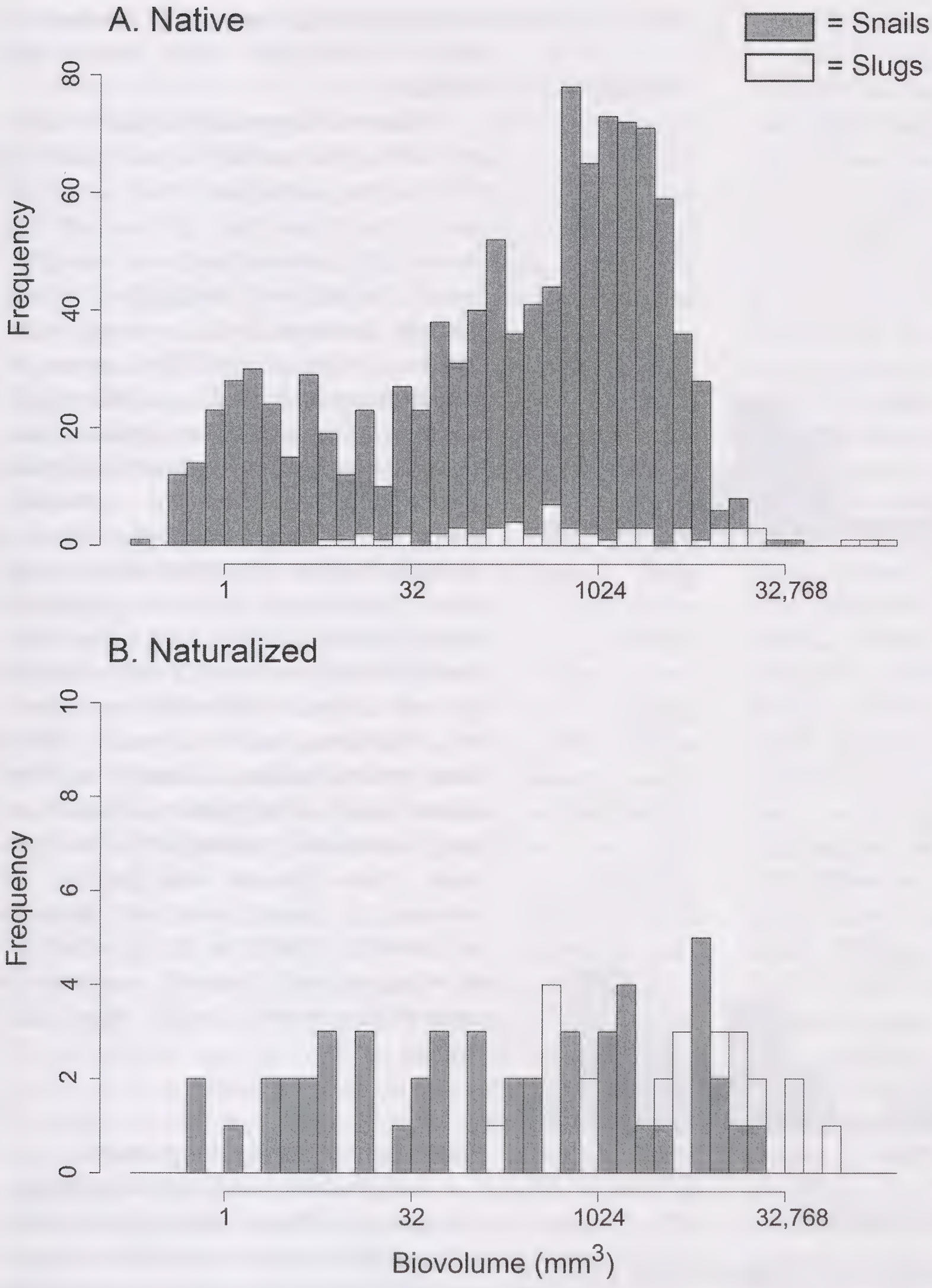

Figure 2: Body size spectra histograms for native and naturalized North American terrestrial gastropods along a $\log_2$ axis, using 0.5 unit bin widths. Filled boxes represent the frequency of snails, while the open boxes represent the frequency of slugs.

and strength of an apertural crest and callus in *Vertigo arthuri* von Martens, 1884 led to the splitting of this entity into six separate taxa (*Vertigo paradoxa* (Sterki, 1900), *V. gouldii basidens* Pilsbry and Vanatta, 1900, *V. hubrichti* (Pilsbry, 1934), *V. brierensis* Leonard, 1972, *V. occulta* Leonard, 1972, *V. iowaensis* Frest, 1991; Pilsbry 1948, Frest 1991), even though they display almost no genetic divergence (Nekola *et al.* 2009). Current analyses on *Pupilla* Leach in Fleming, 1828 across Europe, central Asia, Japan, and North America also indicates profound plasticity in some shell features, rendering invalid many historical species concepts (Nekola *et al.*, in review). However, even in extreme cases such as these, stable conchological traits usually exist to reliably demarcate genetically-distinct species level clades, although these may not be the features that have been historically considered.

Sole use of anatomical features may also lead to faulty conclusions about species-level distinctions. For instance, radular teeth number and configuration are potentially highly unreliable indicators of taxonomic relatedness because they can change with ontogeny (*e.g.*, Bertsch 1976) and are also often under strong ecological selection pressure (*e.g.*, Kesler *et al.* 1986). Also, because gastropods do not exhibit a hard exoskeleton, there is no reason to expect *a priori* that they will possess Arthropod-style lock-and-key genitalia. Rather, gene transfer is at least theoretically possible between individuals with varying genitalic morphologies. DNA sequence analysis demonstrates that at least some anatomically-described North American species are only simple forms within a single, larger variable species (Roth *et al.* 2013). Considerable ontogenetic variability also occurs in many genitalic features (Emberton 1985), with individuals within a single *Catinella* Pease, 1870 population passing through multiple described anatomical 'species' over the course of ontogeny (Brian Coles, *pers. comm.*). Little hard data exists regarding how much genitalic variability exists within and between populations of genetically-validated species-level entities over both space and time. Additionally, considerable potential for observational error exists in measuring various genitalic traits based upon the degree of animal retraction prior to dissection (Emberton 1989).

Molecular data is also not solely capable of resolving valid species-level entities. For instance, mitochondrial (*e.g.*, "bar-code"; Hebert *et al.* 2003) DNA sequence data is problematic in systems with non-zero rates of hybridization, with resulting phylogenetic trees often informing more about the geographic relationships between samples than their taxonomic relatedness (*e.g.*, Shaw 2002, Rubinoff and Holland 2005). Nuclear DNA can also be fallible, as it is possible

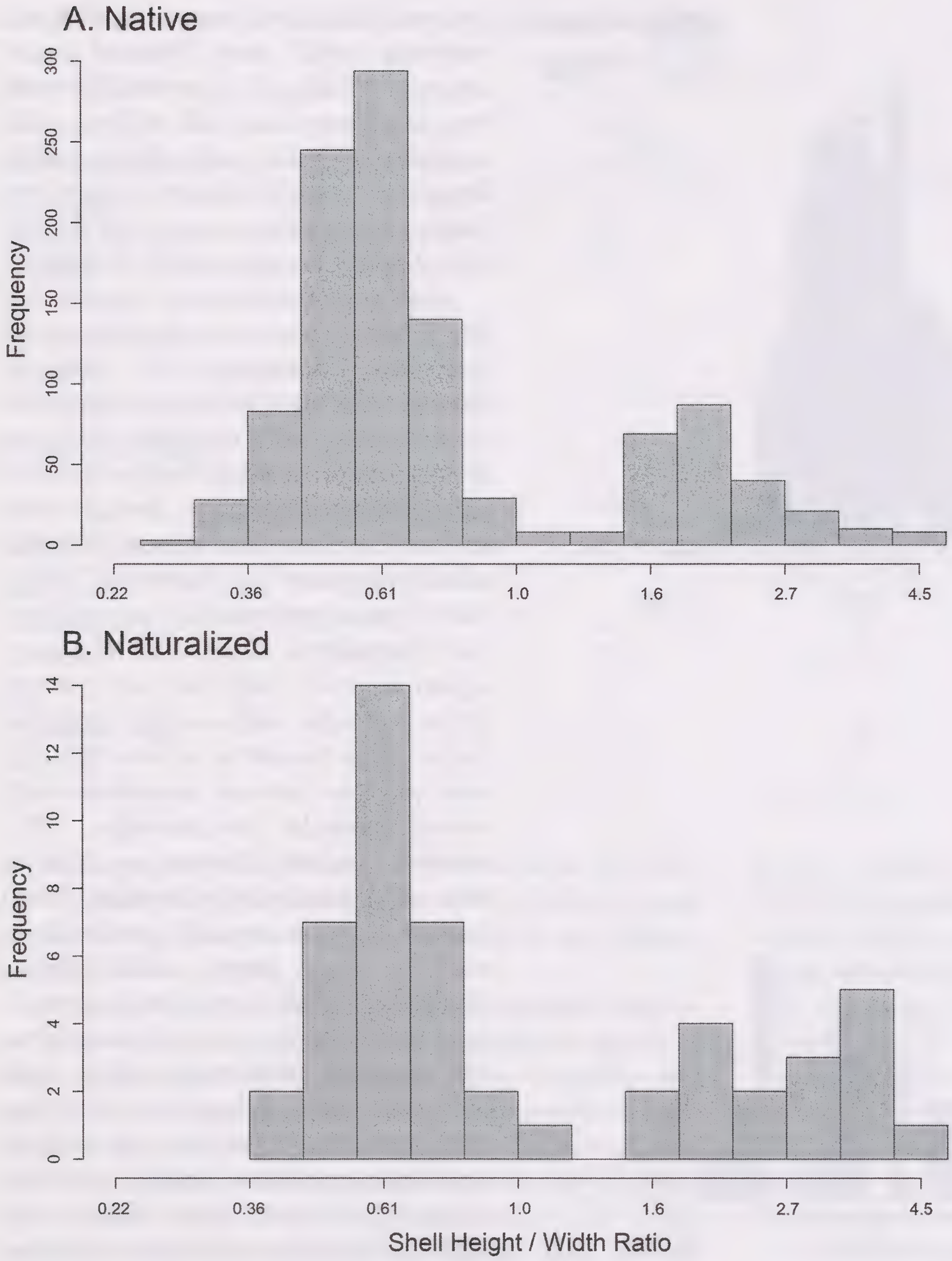

Figure 3: Height:Width ratio distribution for native and naturalized North American land snails along a natural log-transformed axis.

through hybridization and recombination for non-coding regions of one species to become sorted with the coding regions (and mitochondrial DNA) of another. An example of this can be found in Nekola *et al.* (2009) in which one Wisconsin *Vertigo nylanderi* Sterki, 1909 specimen with typical shell features and mitochondrial *cytochrome oxidase subunit 1* and *16S ribosomal RNA* (16S) sequences was found to have an *internal transcribed spacer-2* of the *nuclear ribosomal RNA* (ITS-2) sequence characteristic of *Vertigo gouldii* (A. Binney, 1843).

Current and future revisionary taxonomy must, thus, make use of all data—conchological, anatomical, genetic, and ecological—to identify the boundaries between biologically valid species-level entities.

The most desperately needed revisionary work appears to be the succineids and the western helminthoglyptids, oreohelicids, urocoptids, and *Ashmunella*. The Succineidae demonstrate profound plasticity in not only shell morphology but also genitalic anatomy, and it seems possible that many currently described species are simple ontogenetic and/or ecophenotypic variants within more cosmopolitan entities. For the western helminthoglyptids, oreohelicids, urocoptids and *Ashmunella*, many 'species' share essentially identical shells and habitat requirements, with diagnoses being largely based on geographic isolation in combination with minor variation in genitalic anatomy. Problematically, not only do we not know how much genitalic variation may be expected within these species, because of climatic variation current levels of population isolation can not be assumed for more than a few thousand years. During full-glacials, for instance, the desert southwest becomes much wetter (Pigati *et al.* 2011), potentially allowing currently isolated mesophile or hydrophile populations to come into contact.

Shell shape and body size patterns

Both the native and naturalized terrestrial gastropod fauna is strongly bimodal in terms of shell architecture, with many species being taller than wide or wider than tall, but with few being approximately as tall as wide. This is a global phenomenon in land snails (Cain 1977).

While native land snails also demonstrate a strongly bimodal and left-skewed interspecific body size distribution along a $\log_2$ axis, native slugs demonstrate a roughly lognormal distribution. Naturalized exotic snails possess a roughly uniform distribution with naturalized slugs being again roughly lognormal. These distributions are atypical within the Animalia, with right-skewed interspecific body size distributions prevailing at regional and larger scales (Kozlowski and Gawelczyk 2002) across a diverse suite of taxa groups including nematodes (Kirchner *et al.* 1980), insects (Siemann *et al.* 1996), fish (Knouft 2004), mammals

(Brown and Nicoletto 1991), and birds (Maurer and Brown 1988).

Why should terrestrial gastropods behave so differently? First, it is important to note because both native and naturalized slugs have a minimum biovolume much greater than for snails, the lower mode is expunged from the slug body size distribution (Fig. 2). Thus, there is no reason to assume that different sets of rules govern the two groups. Second, the body size distribution of individuals within the land snail fauna demonstrates the expected right-skewed unimodal distribution across all spatial scales (McClain and Nekola 2008). The underlying cause of these unique patterns, therefore, cannot simply represent rarefaction. Rather, per capita evolutionary rate must be at least partially inversely correlated to body size.

Although a number of factors may be at play (McClain and Nekola 2008), the role of dispersal strategy is likely paramount. Land snails generally possess very poor active dispersal abilities, with many individuals moving perhaps no more than 1–10 m over their lifetime (Schilthuizen and Lombaerts 1994, Hausdorf and Hennig 2003) and being unable to actively cross barriers of only 100–1,000 m (Baur 1988, Schilthuizen and Lombaerts 1994). However, small land snails in particular may also possess excellent passive dispersal abilities: members of the genus *Balea* Gray, 1824, for instance, have been repeatedly carried across 9,000 km of open eastern Atlantic Ocean by migrating birds (Gittenberger *et al.* 2006). Successful movement via passive vectors appears to be inversely correlated with land snail body mass for two principle reasons: First, smaller individuals are less likely to be pulled off of vectors by gravity and aerodynamic drag during migration. Second, the ability to uniparentally reproduce—and , therefore, to found a new population via movement of only a single individual—appears to be common in tiny snails such as *Vertigo* (Pokryszko 1987) and *Carychium* Müller, 1774 (Bulman 1990). To establish a new colony, obligatory outcrossing larger snails will require contemporaneous movement of at least two (likely immature) individuals or of a single adult individual that is storing sperm from prior copulatory activities. As a result, large snails are much more likely to experience isolation, restricted gene flow, and allopatric speciation as compared to small snails. It should, thus, not be surprising that while genera of small snails (such as *Euconulus* Reinhardt, 1883, *Gastrocopta, Pupilla, Punctum, Radiodiscus* Pilsbry and Ferriss, 1906, *Vertigo*) share similar faunas across multiple isolated high elevation mesic forests in the desert southwest, species of large snails (such as *Ashmunella, Holospira* von Marten, 1860, *Humboltiana* von Ihering, 1892, *Sonorella, Oreohelix*) living in these same sites tend to be single-mountain endemics (McClain and Nekola 2008).

Underlying Mathematical Mechanisms

Lastly, POwer-law/LOg-normal (POLO; Halloy 1998) distributions were noted for not only the number of species within families and genera, but also for the number of species described by a given researcher. Such distributions are characterized by a hollow "L"-shaped curve in which most entities are rare, but with a very few entities making up the bulk of the sample. Thus, in the native fauna, over ¾ of species are restricted to only ten families, while six families are represented by only single species. And, the top ten genera encompass over 44% of the entire fauna, while 45 genera are represented by only a single species. Likewise, while Henry Pilsbry alone contributed to description of over ¼ of the entire continental fauna, 61 investigators have described only single species. This type of distribution is common to a wide variety of apparently disparate systems, ranging from kinetic energy of gas molecules and earthquake magnitudes, to word use in written works, income distribution among households, citation rates for scientific papers, Internet web hits, copies of books sold, telephone calls received on a single day, lunar crater diameters, solar flare intensity, deaths in wars, wealth of rich people, surname frequencies, city populations, service times for restaurant glassware, and the first marriage age of Danish and U.S.A. women (Preston 1950, 1981, Newman 2005). These all represent complex dynamical systems, which are composed of many components of many different kinds that interact with each other and their extrinsic environment in many different ways and on multiple spatial and temporal scales, giving rise to complex structures and complicated non-linear dynamics (Nekola and Brown 2007). The presence of such POLO distributions both within the North American land snail fauna, as well as within the community of scientists describing this fauna, indicates that both represent complex systems. Those searching for the ultimate mechanisms underlying these patterns should, therefore, consider wisdom gained by not only by biologists and ecologists, but also complexity scientists.

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